

Chimpanzee Thumb Muscle Cross Sections, Moment Arms and Potential Torques, and Comparisons With Humans

MARY W. MARZKE,^{1,*} R.F. MARZKE,² R.L. LINSCHIED,³ P. SMUTZ,⁴
B. STEINBERG,¹ S. REECE,¹ AND K.N. AN³

¹*Department of Anthropology, Arizona State University, Tempe, Arizona 85287*

²*Department of Physics, Arizona State University, Tempe, Arizona 85287*

³*Orthopedic Biomechanics Laboratory, Mayo Clinic, Rochester, Minnesota 55905*

⁴*Motion Research Associates, Murray, Utah 84107*

KEY WORDS hand; morphology; biomechanics; muscle; fossil hominids

ABSTRACT This study investigates the morphological basis of differences between humans and chimpanzees in the kinematical and dynamical parameters of the musculature of the thumb. It is partly intended to test an hypothesis that human thumb muscles can exert significantly greater torques, due to larger muscle cross-sectional areas or to longer tendon moment arms or to both. We focus on the estimation of the potentials of thumb muscles to exert torques about joint axes in a sample of eight chimpanzee cadaver hands. The potential torque of a muscle is estimated by taking the product of a muscle's physiological cross-sectional area (an estimator of force) with its dynamical moment arm (derived from the slope of tendon excursion versus joint angular displacement, obtained during passive movements of cadaver thumb joints). Comparison of our results with similar data obtained for humans at the same Mayo Clinic laboratory shows significant differences between humans and chimpanzees in potential torque of most thumb muscles, those of humans generally exhibiting larger values. The primary reason for the larger torques in humans is that their average moment arms are significantly longer, permitting greater torque for a given muscle size. An additional finding is that chimpanzees and humans differ in the direction of secondary thumb metacarpal movements elicited by contraction of some muscles, as shown by differences in moment arm signs for a given movement in the same muscle. The differences appear to be related to differences in the musculo-skeletal structures of the trapeziometacarpal joint. *Am J Phys Anthropol* 110:163–178, 1999. © 1999 Wiley-Liss, Inc.

Comparative studies of human and chimpanzee manipulative behavior (Marzke and Shackley, 1986; Marzke and Wullstein, 1996; Marzke et al., 1998) indicate that humans have stronger one-handed precision and power squeeze grips of objects against resistance than do chimpanzees. These observations have led us to propose the hypothesis that thumb muscles whose activity facilitates these manipulative behaviors should be capable of exerting greater torques in

humans than in chimpanzees, because of differences in muscle forces, moment arms, or both. This paper reports the results of an anatomical and biomechanical investigation of muscle torque performed to test this hypothesis in cadaver specimens of chimpan-

*Correspondence to: Mary W. Marzke, Department of Anthropology, Arizona State University, Box 872402, Tempe, AZ 85287-2402. E-mail: mary.marzke@asu.edu

Received 12 August 1997; accepted 23 June 1999.

TABLE 1. Chimpanzee thumb muscle mean fiber length (FL) and standard deviation (SD), volume (VOL), and physiological cross sectional area (PCSA) and SD

Muscle	FL	SD	VOL	SD	PCSA	SD
	(cm)		(cm ³)		(cm ²)	
Adductor pollicis transverse head (APT)	4.9	0.9	6.0	1.4	1.2	0.3
Adductor pollicis oblique head (APO)	3.6	0.6	4.4	1.5	1.3	0.3
Flexor pollicis brevis superficial head (FPBs) ¹	3.5	0.8	5.1	2.4	1.4	0.5
Opponens pollicis (OP)	2.6	0.4	3.8	0.6	1.5	0.4
Abductor pollicis brevis (APB)	3.7	0.7	6.2	3.2	1.8	1.0
Abductor pollicis longus metacarpal portion (APLm) ²	4.7	0.9	15.7	3.1	3.5	1.0
Extensor pollicis longus (EPL)	4.8	1.3	8.7	2.4	1.9	0.7
			TOTAL PCSA:		12.6	

¹ The superficial head of FPB was the only one present in the chimpanzee specimens.

² The full APL muscle PCSA was measured, but only the metacarpal tendon was monitored for excursion.

zee hands, at the Orthopedics Biomechanics Laboratory of the Mayo Clinic (Rochester, MN) and at Arizona State University.

Muscle torque (the capacity of a muscle to rotate a bone around a joint axis) is the product of force (estimated by a muscle's physiological cross-sectional area, or PCSA) and moment arm (the perpendicular distance to a muscle's line of action from the joint rotation center). In seeking data from the literature on these last two quantities in living apes, we find only a few relevant reports. Among these are the studies of Tuttle (1967, 1969, 1970), who measured muscle weights, and of Ricklan (1987), who determined thumb distal phalangeal dimensions relating to the flexor pollicis longus tendon moment arm. To our knowledge, no data on ape PCSA values or moment arms have yet been published.

For humans, however, the situation has become significantly better in recent years. Chao et al. (1989) and Linscheid et al. (1991) have conducted an extensive set of experiments which have provided reliable kinematical estimators of muscle torque potentials. To test our hypothesis concerning relative potential torques of hand and wrist muscles in apes versus humans, therefore, we made a similar set of measurements on eight chimpanzee cadaver hands, which are reported in this paper. This study complements our overall research program on the development of comparative kinematic models that relate bone and joint structures to hand and wrist muscle torque potential in both species. The aims of this program are to find new and improved ways of inferring the

extent of tool-making capability in early hominids from the morphology of their hand bones, our only source of information on this activity vital to human evolution. Valid models of joint function must be built from realistic values of biomechanical parameters, and the data presented here are intended partly to provide such a basis in the living great apes, whose hand structures reflect similarities to humans arising from the two species' close evolutionary relationship, as well as differences related to their differing hand adaptations.

MATERIALS AND METHODS

The experiment reported here was done on the left forelimbs of eight adult fresh chimpanzee cadavers. Three additional chimpanzee cadavers were used in an earlier pilot experiment. Data for the latter are not included in our results, since the protocol for the second experiment was modified to include the insertion of a K-wire to improve stabilization of the trapeziometacarpal joint during passive movement of the proximal phalanx of the thumb.

Estimation of physiological cross-sectional area

Physiological cross sectional area (PCSA) is estimated by dividing the volume of a muscle by its mean fiber length. For each thumb muscle the following protocol, developed by Brand et al. (1981) and used on the human sample at Mayo Clinic (Chao et al., 1989; Linscheid et al., 1991), was applied to the collection of data on muscle fiber length and volume presented in Table 1. First,

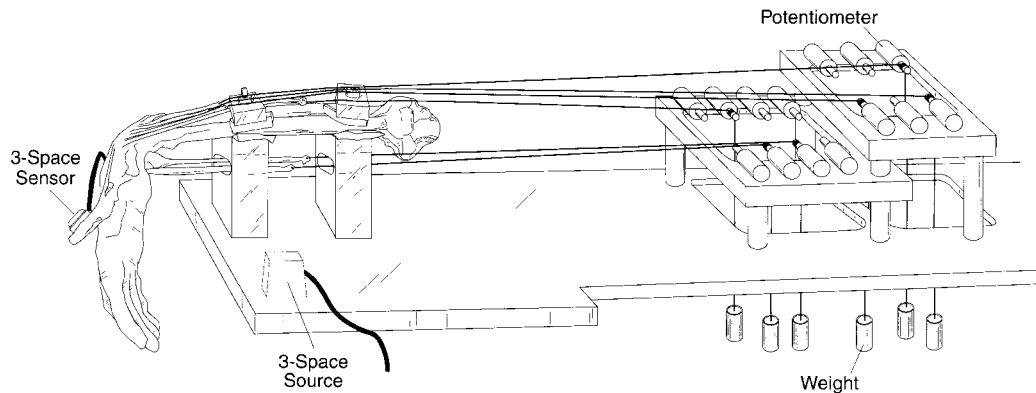


Fig. 1. Apparatus for measuring tendon excursion and joint angle displacement. The specimen is secured in an acrylic vise. Sutures from tendons to the thumb and fingers run to electric potentiometer drums on the right. The source of electromagnetic radiation is at the base of the vise, and the sensor is shown as positioned for thumb metacarpophalangeal joint measurements.

careful inspection and recording were performed of a muscle's attachments, orientation and relationships to other muscles. The muscle is then exposed and cleared of fascia, and the insertion tendon is cut just distal to the point where the muscle fibers terminate. The muscle is next unraveled, without stretching, to expose the parallelepipedon of fibers running from origin tendon to insertion tendon. Fiber length is finally measured with a digital caliper, at three locations, and a mean fiber length is recorded. When separate heads of the muscle have different fiber lengths, mean fiber lengths are taken for each head, and the mean of these means is recorded for the muscle. The separate means are also recorded for future analysis of the muscle's functions.¹ The fibrous portion of the muscle is then lowered into water contained in a graduated cylinder, and the amount of water displaced, measured to an accuracy of ± 0.5 ml, is recorded as muscle volume.

Determination of tendon moment arm lengths

Immediately following removal of the muscle from its insertion tendon, a suture is attached firmly to the tendon, long enough

to run from its attachment on the tendon to a potentiometer drum on an apparatus constructed for measurement of tendon excursion. A tape label is attached to the suture with the name of the muscle.

Moment arm lengths are calculated by the method used on the human sample at Mayo Clinic (An et al., 1991), in which each thumb segment is moved separately while simultaneously measuring (1) the tendon excursion of each muscle and (2) the accompanying angular change of the segment in three planes, which is converted by computer into a change of joint angle. Following the standard model of uniaxial joint rotation produced by tendon excursion, the effective moment arm of a muscle is then the slope of a plot of its excursion versus the joint angle (Landsmeer, 1961; An et al., 1983, 1984, 1991).

The experimental apparatus is illustrated in Figure 1. The dissected forearm is placed in a plastic vise in a pronated position, with the thumb free. The sutures from the tendons run along the direction of muscle pull and are wound around electric potentiometer drums, which are calibrated directly in centimeters and measure tendon excursion during passive movements of the segment [Bourns 10-turn rotational potentiometer (Bourns Inc., Riverside, CA)]. Excursion of each tendon is recorded by its corresponding potentiometer as the segment is moved.

¹The angle of pennation was not measured in this experiment because Zajac (1992) has shown that the muscles of the human forearm and hand are only slightly pennated and thus the angle of their fibers does not significantly affect force or excursion potential.

Weights (averaging 100 g each) are attached to the sutures to prevent their slipping on the drums during thumb movement. Sutures for muscles that are oriented at angles markedly oblique to the long axis of the forearm are routed through pulleys mounted on underlying bone. For muscles that originate from the flexor retinaculum, the sutures are run through tubes anchored to the retinaculum along the lines of action of the muscles. The tubes are lubricated with saline solution to assure smooth movement of the sutures during the experiment. Two trials were done for each movement, during which data were obtained over a period of 5 secs. One investigator (MWM) performed all of the passive segment movements. The plane of each movement passed through the neutral position for the thumb metacarpal relative to the index finger (i.e., with the metacarpal partially flexed and adducted, as it is in the living hand at rest). As discussed in the next section, the moment arms measured in this way were compared with human moment arms similarly obtained by Smutz (1998) for flexion/extension and abduction/adduction motions.

Three-dimensional angular change of the thumb segment in three planes is measured with an electromagnetic tracking device [3Space Tracker System (Polhemus Navigation Sciences Division, McDonnell Douglas Corp., Colchester, VT)], during passive movement of the segment by the investigator. The device has a source of electromagnetic radiation fixed at the base of the supporting structure shown in Fig. 1, in addition to a sensor glued to the thumb nail and adjacent skin. This tracking system for measuring rotation has an accuracy of 0.5° and resolution of 0.1° (An et al., 1988). Testing begins with movement of the thumb metacarpal in abduction/adduction (away from and toward the second metacarpal) at its joint with the trapezium, and then continues in flexion/extension (toward and away from the hypothenar area). During these movements, the proximal and distal phalanges are held in line with the metacarpal shaft. Testing proceeds distally to flexion/extension movements of the proximal phalanx. The trapezio-metacarpal joint is stabilized at this stage by the insertion of a K-wire connecting the

bases of metacarpals 1 and 2, so that tendon excursion specific to movement of the metacarpophalangeal joint may be measured.

The raw sensor data for segment angles and positions in three dimensions, taken during each motion, are transformed by computer into parameters of the equivalent helical, or screw motion of the 3-space sensor's coordinate system. This analysis follows the procedures developed by An et al. (1991), and results in a description in which the purely rotational part of the motion is parametrized by a single angle. This angle is identified as the effective angle of rotation of the joint for the particular motion studied, each value of this angle corresponding to a single value of tendon excursion.

The effective moment arm of each tendon is then the slope of tendon excursion versus the joint's angular displacement curve (An et al., 1991). The reasoning underlying this is especially well-explained by Brand and Hollister (1993, p. 67) in their introduction to hand muscle control of joint postures and movements. These authors note that there is a rule of geometry that connects tendon excursion with angular movement of a joint: "When a lever rotates around an axis through an angle of one radian, every point on the lever moves through a distance equal to its own distance from the axis." Thus the distance (in centimeters) moved by a tendon as a function of joint angle may be used to experimentally measure its effective perpendicular distance from the joint center of rotation. All moment arm values reported in this paper were obtained by first taking an average moment arm for each of the two trials for each specimen, averaging the two trial values, and then taking a mean of the average trial values for the eight chimpanzee specimens.

Calculation of torque potential

With the data on tendon excursion, thumb joint angle changes, and PCSA, one estimates the potential torque of each muscle by simply multiplying the PCSA by the average moment arm. [Another term for potential torque used by Chao et al. (1989) is "joint function potential."] Although the mechanical unit of torque is actually that of force times distance (e.g., Newton-meter or dyne-

cm), since our estimate of force measure here (muscle PCSA) has the dimensions of area, the unit of potential torque used in this paper is one of volume, i.e., cm^3 .

Statistical analysis of the data for PCSA, moment arm, and resultant potential torque

Data for this study were obtained from a sample consisting of only eight chimpanzees, but this is nonetheless a sufficient number to allow the application of statistical techniques that test for significance of the following: (1) observed correlations between biomechanical parameters of the various chimpanzee muscles involved in a given motion, and (2) observed differences between chimpanzees and humans in means and standard deviations of these parameters. This section briefly summarizes the testing methods used.

Resampling (Simon, 1974–1997) is a non-parametric, computer-based approach for dealing with problems of probability and statistical inference, based upon the well-known Monte Carlo technique of generating many possible data sets representing different possible outcomes of an experiment from a single, actual data set. The key step in the procedure is random sampling, in our work always with replacement, of readings taken from the original set of data. The approach is especially well-suited for use with small sets like ours, and is entirely nonparametric in that no assumptions about normalities of distributions are made at any point, i.e., the central limit theorem of probability is never invoked (only illustrated). Rather, a probability distribution is obtained for all statistically distributed (i.e., random) variables, based upon the assumption of random resampling of the original data set (or sets). Since we have no a priori knowledge concerning the underlying distributions of our biomechanical data, either in humans or in chimpanzees, we decided that this approach to the statistical treatment of our data was most appropriate for our purposes.

We applied it principally to three problems. First we estimated probability values (p -values) for our observed correlations in a given motion among pairs of muscles in the chimpanzees, for the variables PCSA, mo-

ment arm and resultant potential torque (see Simon, 1974–1997, Chapter 23). Correlations were judged to be significant when their probability of occurrence under resampling was found to be .015 or less.

We next applied resampling to a comparison of chimpanzees with humans for evidence of significant differences in mean moment arm, for each muscle. A sample of seven measured human moment arm values was obtained from the original data for the paper by Smutz et al. (1998). For the comparison, the values and means of these human moment arms were multiplied by a correction factor, in order to partly control for average chimpanzee–human body mass differences. Our rationale for assigning this factor is as follows. To begin with, the ratio of pooled male and female chimpanzee to pooled male and female human mean body weights is approximately 0.9, as reported in Rafferty (1998, Table 1), drawn from Jungers and Susman (1984) for chimpanzees, and from a personal communication from Ruff to Rafferty (1998) for humans. To have used this number directly in correcting for mass differences, however, would have been inconsistent with the approximate proportionality of body weight to body volume, not (usually) to segment length. It appeared to us that, since volume is proportional to the cube of length in general, the preferable procedure in interspecies comparison is to correct lengths such as moment arms via the cube root of the mass ratio. Thus the data of Smutz et al. (1998) for human moment arms, listed in Table 2 of this paper, were multiplied by 0.965 for statistical tests.

These weight-corrected human moment arm data were then pooled with the actual chimpanzee data, following standard procedure for two-sample testing as described in Bruce et al. (1997) (see also Mooney and Duval, 1993; and Edgington, 1995). The probability distribution of the difference between human and chimpanzee sample means was obtained, under the hypothesis of random resampling, to give a p -value estimate for the mean difference between the actual human and chimpanzee data sets. This p -value for the observed difference is considered by us to be more informative than the simple comparison of means and standard

TABLE 2. Mean chimpanzee thumb muscle physiological cross sectional areas (PCSA), moment arms (MA) and potential torque (PT) for abduction/adduction (AB/AD) and flexion/extension (F/E) at the trapeziometacarpal (TMC) joint, and for flexion/extension (F/E) at the metacarpophalangeal (MP) joint¹

Muscle	PCSA (cm ²)	TMC AB/AD				TMC F/E				MP F/E			
		MA (cm)	SD	PT (cm ³)	SD	MA (cm)	SD	PT (cm ³)	SD	MA (cm)	SD	PT (cm ³)	SD
APT	1.2	3.3	0.8	3.9	1.3	-1.2 ²	1.8	-1.7	2.3	NA			
APO	1.3	1.5	0.4	1.8	0.6	-0.1 ³	0.5	-0.2	0.6	0.4	0.3	0.5	0.5
FPBs	1.4	0.2	0.2	0.3	0.4	1.1	0.4	1.5	0.7	0.4	0.1	0.6	0.2
OP	1.5	0.5	0.4	0.7	0.7	0.7	0.4	1.1	0.7	NA			
APB	1.8	-0.7	0.7	-1.5	2.0	1.3	0.3	2.2	1.4	0.2	0.1	0.4	0.3
APLm	3.5	-0.4	0.3	-1.5	1.3	0.3	0.1	1.1	0.7	NA			
EPL	1.9	-0.2	0.3	-0.5	0.8	-1.0	0.4	-1.9	1.3	-0.6	0.1	-1.2	0.5

¹ Positive moment arms are flexion and adduction; negative moment arms are extension and abduction.

² $N = 7$; the moment arm was negative in six individuals and positive in one.

³ $N = 7$; the moment arm was negative in five individuals and positive in two.

deviations, which are most appropriate for normally distributed variables.

Finally, resampling was applied to the similar problem of assessing significances of observed differences between the two species with regard to PCSA and potential torque. Here, however, the approach was complicated by the absence of individual data for PCSA in the human sample studied by Smutz et al. (1998), whose measurements of muscle function had focused mainly on moment arms. For chimpanzees, we had obtained a datum for PCSA and one for moment arm for each individual in our sample of eight, and the resulting potential torque was simply the product of these two. For humans, the only information available for estimation of potential torques in the human sample was a known average value of PCSA for humans obtained previously in other studies (Linscheid et al., 1991; Chao et al., 1989). Use of this average, to multiply each of the measured moment arm values from Smutz's data, yielded a probable set of values of potential torque for each human, whose average was simply the product of the Linscheid-Chao average PCSA with our sample-average moment arm. This also gave an estimate of potential torque standard deviation.

However, this procedure did not furnish assessments of the significance of the observed differences between humans and chimpanzees in average potential torques, along the lines of our assessment of differences in average moment arms. We strongly desired to make such assessments, if possible, for all three biomechanical parameters, especially

potential torque. For this purpose, we decided to simply generate a random sample of representative possible human values, using standard statistics computing capabilities, from a normal (Gaussian) distribution having the known Linscheid-Chao mean and standard deviation. We then used these pseudo-values to obtain p -values, but only in mean difference significance assessments, not in any assessment of correlation significance. The p -values given for potential torque difference significance, in the Results section below, are those obtained in this way. They are subject to greater uncertainty than our reported difference significance for moment arm, and we have thus interpreted them more conservatively.

RESULTS

Chimpanzee muscle parameters

Sample means and standard deviations for the fiber length (FL), volume (VOL), and physiological cross sectional area (PCSA) of each muscle of the chimpanzee thumb are given in Table 1.

From Table 1 it is evident that differences between muscles in mean fiber length (FL) are consistent with differences in range of motion at the joints crossed by the muscles. For example, the two extrinsic muscles [abductor pollicis longus metacarpal portion (APLm) with 4.7 cm fiber length and extensor pollicis longus (EPL) with 4.8 cm] cross both the wrist and the trapeziometacarpal joint, and the EPL continues across two more joints to the distal phalanx. The transverse adductor pollicis muscle [APT] 4.9

TABLE 3. Significant correlations ($p < .01$) among pairs of chimpanzee muscles for potential torque (PT), moment arms (MA) and physiological cross-sectional area (PCSA)

PT (TMC AB/AD)	C. C. ¹	PT (F/E)	C. C.	MA (TMC AB/AD)	C. C.	MA (TMC F/E)	C. C.	MA (MP F/E)	C. C.	PCSA	C. C.
EPL/APLm	0.76									EPL/APLm	0.89
EPL/APB	0.93			EPL/APB	0.93						
FPBs/OP	0.80										
APT/OP	0.80										
		APB/OP	0.74								
				EPL/APO	-0.76						
						APB/APT	-0.89				
						APLm/OP	-0.72				

¹ Correlation coefficient.

cm] bridges the wide web space between the thumb and the index and third fingers and draws the thumb from an abducted position toward the palm. The opponens pollicis (OP), with the shortest fiber length (2.6 cm), crosses a single (trapeziometacarpal) joint.

The PCSA of APLm is 28% of total thumb muscle PCSA, which is substantially larger than that of any other thumb muscle. The difference may be explained by the fact that the muscle also attaches to the trapezium and moves the wrist as well as the thumb. The mean values for PCSA of the remaining thumb muscles cover a relatively small range, from 1.2 to 1.9 cm², in the order APT < APO < FPB < OP < APB < EPL. Note that extensor pollicis brevis fibers, which in humans lead to a tendon inserting into the proximal phalanx, were not found in any of the eight chimpanzee specimens in our sample.

In Table 2 we give means and standard deviations of the moment arms. The mean chimpanzee potential torques are the products of mean PCSAs (also given in this table) with these experimental mean moment arms.

At the trapeziometacarpal joint the moment arm and potential torque for adductor pollicis oblique head (APO) adduction are substantially larger (by 15 and 9 times respectively) than those for extension. The adductor pollicis transverse head (APT) moment arm and potential torque for adduction are more than double those for extension. The moment arm and potential torque for flexor pollicis brevis superficial head (FPBs) flexion are 5.5 times larger than for adduction, and the EPL extension moment

arm and potential torque are substantially larger than for abduction. In all these cases, therefore, the names of these intrinsic muscles clearly reflect their primary functions. An exception is the abductor pollicis brevis (APB) muscle, whose flexion moment arm and potential torque exceed those for abduction.

The trapeziometacarpal adductor moment arm of APT is more than double that of the oblique adductor (APO) and its extensor moment arm is 12 times that of APO. The APLm has relatively small moment arms for metacarpal abduction and extension. Although the muscle has a markedly large PCSA, its potential trapeziometacarpal torque is only average among the muscles for movements in both planes, because its moment arms for these actions are not exceptionally large.

Chimpanzee muscle correlations

Table 3 shows significant correlations ($p < .01$) among several pairs of muscles in the chimpanzee sample for potential torque (five pairs, of which four are positive correlations for movements in the trapeziometacarpal AB/AD plane), moment arms (two pairs for each trapeziometacarpal movement plane) and PCSA (one pair). The single PCSA pair (EPL/APLm) is also one of the potential torque pairs correlated for trapeziometacarpal movement in the AB/AD plane. The EPL and APB muscles are positively correlated in both their moment arms and potential torque for trapeziometacarpal movement in the AB/AD plane. The other three significant moment arm correlations

TABLE 4. Mean human physiological cross-sectional areas (PCSA) of thumb muscles

Muscle	PCSA ¹	SD	Sample size
APT	0.9	0.4	7
APO	3.1	0.9	7
FPBd ²	0.9	0.6	7
Pl ³	0.8	0.5	7
FPBs	1.4	0.8	7
OP	2.6	1.3	7
APB	1.6	0.6	7
APL	3.9	2.0	4
EPL	1.9	0.8	4
EPB ⁴	1.3	0.7	4
FPL ⁵	5.1	2.6	4
Total PCSA:	23.5		

¹ PCSA data are from Linscheid et al. (1991) for the first seven muscles and from Chao et al. (1989) for the others.

² FPBd: Flexor pollicis brevis deep head.

³ Pl: First palmar interosseus.

⁴ EPB: Extensor pollicis brevis muscle.

⁵ FPL: Flexor pollicis longus muscle.

are negative (EPL/APO, APB/APT, and APLm/OP).

DISCUSSION

Physiological cross-sectional areas

Comparison of the chimpanzee mean muscle PCSA data (Table 1) with mean PCSA data obtained from the literature for humans (Tables 4 and 5) shows marked differences. Total thumb muscle PCSA measured for humans is nearly double that of chimpanzees. The primary contributors to the difference are the flexor pollicis longus (FPL) and APO in humans. It is well known that the FPL is not usually present as a functioning muscle in chimpanzees (Marzke, 1971). This muscle comprises 22% (5.1/23.5 cm²) of the total thumb muscle PCSA in the human sample (see Table 4). The oblique portion of the human adductor pollicis muscle is significantly larger than in the chimpanzees, with a mean PCSA more than double that of the chimpanzees (Table 6). The average human OP is also significantly larger. Two intrinsic muscles that are normally distinguishable in humans but not in chimpanzees, the first palmar interosseus (P1) and the deep head of the flexor pollicis brevis muscle (FPBd), contribute an additional 7% to the overall human PCSA. They are elements of another muscle, probably of the oblique adductor pollicis muscle (Linscheid, 1991), which have become differentiated in humans, perhaps in adaptation to

requirements for greater dexterity in one-handed manipulation of objects (Marzke et al., 1998). It is interesting to note that the oblique adductor, together with these separate elements, contributes 20% to total PCSA, compared with 10% in the chimpanzees, and 42% of total intrinsic muscle PCSA (4.8/11.3 cm²), compared with 18% (1.2/7.2 cm²) for the chimpanzee sample. In contrast, the more distal, transverse adductor pollicis fibers (APT) form only 8% of total intrinsic PCSA in the human sample (0.9/11.3 cm²) compared with 17% (1.2/7.2 cm²) in the chimpanzees.

The human OP constitutes nearly a quarter (23%) of the total intrinsic muscle PCSA (2.6/11.3 cm²) compared with 21% in the chimpanzee sample (1.5/7.2 cm²), while the FPBs and APB constitute smaller proportions of the intrinsics in both species.

Moment arms and potential torques

Comparison of chimpanzee mean moment arms and potential torques with means determined by Smutz et al. (1998) for humans (see Table 5)² shows even more numerous and marked differences. Mean values that differ significantly between the two species are given in Table 6.

Opponens pollicis muscle. The most striking potential torque differences between the chimpanzee and human samples are in the OP, APO and APT muscles. The human OP is significantly larger in potential torque for movements in both the abduction/adduction and flexion/extension planes, and in both variables contributing to torque: the PCSA and the moment arms for movements in both planes. The muscle functions in humans as a flexor and abductor of the thumb metacarpal, movements that draw the pad of the thumb into opposition to the pads of all four fingers. This combination of movements is fundamental to the human ability to hold and control large objects in one hand alone. It is interesting to note that in the chimpanzees the OP functions as a

²It is emphasized here, and noted in Table 5, that the potential torque estimates are products of mean PCSAs from one sample of specimens (including four reported by Chao et al., 1985, supplemented by three more reported by Linscheid et al., 1991) and mean moment arms from another sample of specimens dissected in the same laboratory (Smutz, 1998).

TABLE 5. Mean human thumb muscle physiological cross sectional areas (PCSA), mean moment arms (MA) and estimated potential torque (PT) for abduction/adduction (AB/AD) and flexion/extension (F/E) at the trapeziometacarpal joint (TMC), and for flexion/extension (F/E) at the metacarpophalangeal joint (MP)¹

Muscle	PCSA (cm ²)	TMC AB/AD				TMC F/E				MP F/E			
		MA (cm)	SD	PT (cm ³)	SD	MA (cm)	SD	PT (cm ³)	SD	MA (cm)	SD	PT (cm ³)	SD
APT	0.9	1.9	1.2	1.7	0.8	3.4	0.6	3.1	0.6				
APO	3.1	1.6	1.0	5.0	2.7	2.6	0.9	8.1	0.9	0.6	0.3	1.9	1.2
FPBs	1.4	-1.0	0.5	-1.4	1.5	1.3	0.5	1.8	0.5	0.7	0.1	1.0	0.6
OP	2.6	-0.6	0.7	-1.6	1.4	1.2	0.3	3.1	0.3	NA			
APB	1.6	-1.7	0.5	-2.7	1.0	0.3	0.5	0.5	0.5	0.3	0.4	0.5	0.7
APLm	3.9	-1.0	0.1	-3.9	1.5	-0.7	0.2	-2.7	0.2	NA			
EPL	1.9	0.8	0.3	1.5	0.4	-0.9	0.3	-1.7	0.3	-0.9	0.1	-1.7	0.6

¹ PCSA data are from Table 1. MA data are derived from plots for each of six individuals in the human sample for TMC AB/AD and seven individuals for TMC F/E and MP F/E.

TABLE 6. Muscles differing significant ($p < .01$) between the chimpanzee (*Pan*) and human (*Homo*) samples in mean PCSA, moment arms and potential torque¹

Muscle	Genus	PCSA (cm ²)	TMC AB/AD		TMC F/E		MP F/E	
			MA (cm)	PT (cm ³)	MA	PT	MA	PT
APT	<i>Pan</i>	1.2	3.3	3.9	-1.2	-1.7		
	<i>Homo</i> ²	0.84	1.83	1.54	3.28	2.76		
APO	<i>Pan</i>	1.3		1.8	-0.1	-0.2		0.5
	<i>Homo</i> ²	2.89		4.32	2.51	7.25		1.71
FPBs	<i>Pan</i>		0.2	0.3				
	<i>Homo</i> ²		-0.97	-1.26				
OP	<i>Pan</i>	1.5	0.5	0.7	0.7	1.1		
	<i>Homo</i> ²	2.42	-0.58	-1.40	1.16	2.81		
APB	<i>Pan</i>		-0.7		1.3	2.2	0.2	
	<i>Homo</i> ²		-1.64		0.29	0.43	0.29	
APLm	<i>Pan</i>		-0.4		0.3	1.1		
	<i>Homo</i> ²		-0.97		-0.68	-2.47		
EPL	<i>Pan</i>		-0.2	-0.5			-0.6	
	<i>Homo</i> ²		0.77	1.36			-0.87	

¹ Human values (from Tables 4 and 5) are adjusted here for body size difference from chimpanzees (see text).

² These *Homo* PCSA and MA values are weight-corrected to two decimal places in order to give agreement with the weight-corrected PT, which is equal to $0.9 \times$ the corresponding uncorrected PT from Table 5.

flexor and as an adductor rather than an abductor of the thumb. This difference in abduction/adduction activity is indicated by the difference in sign between chimpanzee and human mean values for the abduction/adduction moment arm (see Table 7).

Adductor pollicis (oblique), adductor pollicis (transverse) and flexor pollicis brevis (superficial) muscles. The chimpanzee APO has significantly smaller potential torque than the human APO, for both adduction and flexion of the trapeziometacarpal joint and flexion of the metacarpophalangeal joint. The significantly larger human PCSA contributes to the differences in torque, supplemented in trapeziometacarpal flexion by a significantly larger moment arm. In fact, the human APO flexion moment arm and potential torque are larger than the human adduction moment arm and

TABLE 7. Muscles that differ in moment arm sign and in direction of pull on the thumb at the trapeziometacarpal joint

Muscle	Genus	TMC AB/AD	TMC F/E	Function
		MA (cm)	MA (cm)	
FPBs	<i>Pan</i>	0.2		adduction
	<i>Homo</i>	-1.0		abduction
OP	<i>Pan</i>	0.5		adduction
	<i>Homo</i>	-0.6		abduction
EPL	<i>Pan</i>	-0.2		abduction
	<i>Homo</i>	0.8		adduction
APT	<i>Pan</i>		-1.2	extension
	<i>Homo</i>		3.4	flexion
APO	<i>Pan</i>		-0.1	extension
	<i>Homo</i>		2.6	flexion
APLm	<i>Pan</i>		0.3	flexion
	<i>Homo</i>		-0.7	extension

potential torque, indicating that flexion is the primary action of the muscle at the trapeziometacarpal joint. As with OP, the moment arm signs differ between the two species, this time for trapeziometacarpal

flexion/extension (Table 7). In this case, the negative value indicating metacarpal extension by APO in chimpanzees (the secondary function of the muscle) is extremely small (-0.1 cm) and is a mean of positive and negative moment arms that range in length from -0.6 to $+0.8$ cm. The chimpanzee APO tendon apparently lies so close to the center of joint rotation for flexion/extension that it varies in action from one individual to another. In our sample it extended the metacarpal in the majority of specimens (5) and flexed it in the remaining two for which we have data. The human moment arm mean of 2.51 cm (Table 6) is substantially larger than any of the chimpanzee values, placing it outside the chimpanzee range by several standard deviations. This variability in the chimpanzee moment arm is further discussed in the section below on moment arm signs.

Human thumb flexion is further enhanced by the APT, which has significantly larger potential flexion torque in spite of a smaller PCSA, due to a larger flexion moment arm. Like APO, APT acts primarily as an extensor in the chimpanzees (Table 7), with a moment arm sign generally, but not always negative, ranging in our sample from -4.3 to $+1.3$ cm.

Regarding FPBs, its action in chimpanzees is to adduct, while the human FPBs acts as an abductor, with a significantly larger moment arm and potential torque for movement in the abduction/adduction plane. The very small mean size of the chimpanzee FPB adduction moment arm again indicates that the muscle lies close to the center of rotation for trapeziometacarpal abduction/adduction, and probably contributes relatively little to movement in this plane.

The importance of the adductor and short flexor muscles in human firm precision pinch grips has been emphasized by Brand and Hollister (1993), who note how the muscles together play an essential role in stabilizing both joints while the FPL flexes the distal phalanx. The stronger the contraction of the FPL, the more important is the role of these intrinsic muscles in maintaining the posture and stability of the more proximal joints. This is consistent with our EMG study of

thumb muscle recruitment during Oldowan hard hammer tool manufacture (Marzke et al., 1998), which has shown that these intrinsic muscles in fact tend to be more heavily recruited than FPL during forceful precision pinch grips against strong resistance.

Abductor pollicis longus and abductor pollicis brevis muscles.

There are significant differences between chimpanzees and humans for trapeziometacarpal abduction moment arms of APLm and APB. The human moment arms are primarily responsible for trapeziometacarpal abduction potential torque that is more than two times the chimpanzee potential torque, since the PCSA is quite similar in the two species (see Tables 2 and 5). The long abductor is second only to APO in relative potential torque of the human thumb muscles in the abduction/adduction plane. The human APLm also has a significantly longer moment arm for trapeziometacarpal movement in the flexion/extension plane, contributing to potential torque that is significantly larger than that of the chimpanzees. (Our data indicate that the muscle extends the thumb in humans, whereas it flexes the thumb in the chimpanzees.)

The short abductor muscle positions the thumb in opposition to the fingers for both precision and power grips in humans (Brand and Hollister, 1993), and together with the APLm contributes to stabilization of the trapeziometacarpal joint. During forceful pinch the APLm plays an important role in stabilizing the trapeziometacarpal joint against the pull of the adductor and short flexor, while the latter muscles (together with the short abductor) flex the metacarpophalangeal joint (Brand and Hollister, 1993).

Extensor pollicis longus muscle. The EPL adducts rather than abducts the thumb metacarpal in the human sample, with a significantly larger torque due primarily to a significantly larger moment arm. The mean moment arm in the chimpanzees is very small, indicating a relatively minor contribution to trapeziometacarpal abduction. At the metacarpophalangeal joint, the human long extensor has a significantly larger moment

arm for extension, but potential torque is not significantly larger.

Additional observations. The larger moment arms found for many of these muscles in humans provide them with greater potential torques, for a given muscle force. Alternatively, the human hand may be viewed as having evolved in such a way that it can produce large output torques without the need for very large muscle forces, or PCSA. In this connection, it is interesting to note that there is a larger number of significant differences between the species in moment arms than in physiological cross sectional areas, and one may ask why this should be so. The answer is that small values of muscle PCSA are desirable, because analysis shows that for a given external load on the hand, the joint constraint forces (axial and lateral) required for joint stabilization will generally decrease with increasing moment arms, but will increase with increasing muscle forces. The constraint forces are supplied by the ligaments, capsule, and other elements of the joint, and there are limits to the forces that these elements can produce. For example, Cooney and Chao (1977) warn that "degenerative changes and occasionally rupture" of ligaments may even be anticipated in repetitive application of large external loads. These authors also show that the activities of the modern human hand subject it to loads that may result in such limiting joint stresses, especially in the thumb carpometacarpal joint.

During the hand's evolution, one particularly important activity would have been the manufacture of stone tools, which requires firm, one-handed precision grips of the stones against strong resistance, i.e., the capability for both hands to exert large torques. Electromyographic (EMG) studies have shown that during tool making with these grips very high peak activity levels in the intrinsic thumb muscles are elicited (Marzke et al., 1998). Similarly, very high peak activity of the flexor pollicis longus muscle has been observed during manipulation of cylindrical objects, which require a firm squeeze grasp (Marzke et al., 1998). It could even be argued, therefore, that the large moment arms of human thumb muscles have resulted from

the development of our distinctive ability to maintain for long time periods forceful precision and squeeze grips of objects, with the thumb and fingers of one hand. Simply increasing muscle forces for the performance of such tasks is ruled out, as we have seen, by the physical limits on constraint forces that joints can produce.

We also point out that there are two exceptions, found during our study, to the human advantage in moment arm lengths and potential torques. These are the significantly larger chimpanzee APT moment arm and potential torque for trapeziometacarpal adduction, and the significantly larger chimpanzee moment arm and potential torque for trapeziometacarpal flexion by the APB. For APT, the PCSA is also significantly larger, resulting in a torque potential more than double that of humans. The moment arm is the stronger contributor to this difference in potential torque. These departures from the trend toward smaller moment arms and potential torque in the chimpanzee thumb muscles are understandable, however, when one considers the chimpanzee's frequent gripping of objects between the thumb and the side of the lower part of the long index finger (Christel, 1993; Marzke and Wullstein, 1996). This is associated with skeletal features of the thumb that are apparently specialized for this grip (Marzke and Wullstein, 1996). The significantly larger trapeziometacarpal flexion moment arm and potential torque of APB complement the emphasis on chimpanzee adduction by opposing the tendency of APT to extend the thumb during adduction. This is a secondary function which itself distinguishes the chimpanzees from humans, since the adductor muscle moment arm has a negative sign in the flexion/extension plane.

Differences in moment arm signs indicating effects of thumb position on muscle function

Table 7 summarizes differences between the chimpanzee and human samples in aspects of muscle actions that are reflected by differences in moment arm signs in Tables 2 and 5. In all cases, the sign differences are for what might be called the secondary functions of the muscles. For example, the

chimpanzee adductor muscles tend to have negative flexion/extension moment arm values, while humans have positive ones, indicating that in chimpanzees these muscles extend rather than flex the first metacarpal. The chimpanzee short flexor and opponens muscles adduct rather than abduct the metacarpal, the long abductor flexes the metacarpal and the long extensor abducts the metacarpal. Although the human APB does not have the reverse sign for flexion/extension, it does lie very near the joint center of flexion/extension rotation. A source of these unexpected differences is suggested by the extensive work of Ou (1979), who finds that variations in the angle of the human thumb principal rotation axes for primary movements relative to the planes of the other metacarpals are associated with variations in the accompanying secondary movements. For example, the adductor muscles flex the thumb when the thumb is in the plane of the palm, but as the thumb is rotated out of this plane palmarly, these muscles have an increasing effect in extension. It is likely, then, that the chimpanzee thumb is positioned and oriented differently, as Napier (1964), Lewis (1989), and Sarmiento (1994) predicted, and that this difference alters the relationships of muscle origins and insertions to the extent that secondary actions of the muscles are sometimes even the reverse of those in humans. The moment arms tend to be quite small for these secondary movements (with the exception of those for the human adductors), indicating that the lines of action of the tendons lie near the joint center of rotation for these movements and thus near the sign crossover predicted by Ou (1979). We consider this as the probable explanation for our surprising observations that even the signs of the moment arms (and thus the movements caused by the muscles) may vary among individuals. We surmise that this may arise either because the position of the thumb relative to the palm varies or because small variations occur in the orientation of the plane of rotation.

The difference between chimpanzees and humans in secondary movements of these muscles may simply be a by-product of adjustments in chimpanzee wrist skeletal configurations to the accommodation of large

extrinsic flexor tendons in the carpal tunnel. However, it is interesting to note the following. (1) Both the FPB and OP function as adductors in the chimpanzee, supplementing the well-developed APT for adduction. (2) The trapeziometacarpal abduction/adduction potential torques of FPB and APT are strongly correlated with that of OP (see next section). (3) Finally, the thumb/index finger pad-to-side grip, involving adduction/flexion of the thumb trapeziometacarpal joint, is the manipulatory grip used most frequently by chimpanzees (Christel, 1993).

Correlated muscle potential torques, moment arms and physiological cross sectional areas

All five significant potential torque correlations for the chimpanzees are positive (EPL/APLm, EPL/APB, FPBs/OP and APT/OP for trapeziometacarpal movements in the abduction/adduction plane and APB/OP for trapeziometacarpal flexion). Each pair shares the same function, and the function for four of the pairs is trapeziometacarpal abduction/adduction. As noted above, OP correlates with both APT and FPBs, each of them being a thumb adductor in the chimpanzee; this is an important element of the pad/side holding grip of chimpanzees. Both the APB and EPL abduct the thumb, and together with the APLm (which also abducts and is correlated with EPL) perhaps stabilize the metacarpophalangeal joint during pad/pad holding.

A significantly large negative correlation was found for the moment arms of EPL/APO in the abduction/adduction plane. This is consistent with the contrasting functions of the two muscles; EPL is an abductor and APO an adductor in the chimpanzee sample. The moment arms of two muscle pairs are negatively correlated for trapeziometacarpal flexion/extension: APB/APT and APLm/OP. The APB and APT muscles cause the contrasting movements of extension and flexion respectively, but the APLm and OP are both flexors in the chimpanzee sample.

Two pairs of muscles have positive correlations for two parameters: EPL and APLm for PCSA and potential torque, and EPL/APB for trapeziometacarpal abduction/adduction moment arm and potential torque.

Significant moment arm correlations were found in the comparative human sample among three pairs of muscles for trapeziometacarpal abduction/adduction, with the following coefficients of correlation: EPL-APLm (0.81), EPL-FPBs (0.83), and EPL-APO (0.76). The chimpanzee sample shares a significant EPL-APO correlation, but it is negative in the chimpanzee and positive in the human sample. The other two significant muscle correlations in humans are not shared by the chimpanzee sample.

Possible new predictors of potential muscle torque and tool-making capabilities in fossil hominid bones

Evidence in this experiment for the proportionately large contribution of moment arms to variations between the two species in muscle torque potential suggests that the development of models to predict precision and power gripping capabilities in fossil hominid hands should emphasize the measurement of skeletal configurations affecting muscle moment arm lengths and directions of muscle pull at the joints. Although we unfortunately lack skeletal data on the chimpanzee sample reported in this paper, we suggest that the search for predictors start by focusing on skeletal configurations associated with certain muscles. These are ones that have been shown in our complementary EMG and biomechanics experiments to be both strongly recruited during specific manipulative activities and significantly different in moment arm lengths between humans and other catarrhine species. Measurement and quantitative comparisons of these skeletal configurations is becoming possible with recent developments in techniques for three-dimensional imaging.

The initial step toward obtaining skeletal predictors of moment arms is to identify skeletal features that appear to be the principal sources of differences in muscle function among species. We cite three examples of possible skeletal configurations here, in the case of chimpanzee and human hands. First, a major factor affecting the moment arms and functions of the muscles acting at the trapeziometacarpal joint appears to be the position of the thumb metacarpal rela-

tive to the volar surfaces of the second and third metacarpals from which the muscles arise. The bases and lower shaft of the latter metacarpals flare forward in humans, along with the trapezoid, bringing the adductor muscle attachments anterior to the flexion/extension axis of the trapeziometacarpal joint. The flexion/extension axis of the trapeziometacarpal joint may also be oriented at a greater angle to the plane of the palm, contributing to the differences between chimpanzees and humans in the direction of pull of the thumb muscles. Systematic, quantitative comparative analysis of this carpometacarpal unit is in progress, and may uncover the features that facilitate a strong flexor contribution of the APO muscle to firm precision grips in humans.

The second possible skeletal configuration involves the moment arms of the short flexor and the oblique adductor muscle at the metacarpophalangeal joint of the thumb. Both the FPB and the APO tendons cross the anterior margin of the metacarpal head on their way to insertion into the joint capsule, sesamoids in the capsule and the radial and ulnar sides of the base of the proximal phalanx. The degree of anterior projection of the metacarpal head joint surface relative to the joint center of rotation thus will strongly affect the length of the moment arm.

A third example is found at the distal interphalangeal joint of the thumb, where the FPL muscle inserts. There is normally a relatively large excavation at the volar base of the distal phalanx in humans, which accommodates a sesamoid bone in the distal interphalangeal joint capsule when the distal phalanx is flexed (Wilkinson, 1953; Marzke et al., 1998). Much has been made of this excavation, because it appears in the distal thumb phalanges of the Olduvai *Homo habilis* reported by Napier (1962), of *Paranthropus* reported by Susman (1988 a,b; 1989), and of the Sterkfontein thumb reported by Ricklan (1990). It was assumed by these authors (and also by Marzke, 1997) that the excavation was occupied by a large flexor pollicis longus tendon, reflecting a large associated muscle. Since a functioning FPL muscle is regularly present in humans but not in great apes (see Marzke, 1971), it has been further assumed that tendon insertion

evidence for a large flexor pollicis longus muscle reflects a human-like ability for stone tool making. Recent dissections in our laboratory indicate, however, that the size of the excavation is more likely to reflect the size of the sesamoid and thereby the size of the FPL moment arm rather than the size of the muscle itself (Marzke et al., 1998).

In addition to hand skeletal features governing relative moment arm sizes, it also may be possible to find skeletal indicators of relative PCSA, which would then provide a basis upon which to draw inferences concerning relative potential muscle torques. Muscle stress markers on the skeleton are one such indicator. It has been routinely assumed that differences among individuals in the size of muscle markings on bone reflect differences in muscle force potential. The assumption is currently being tested in our laboratory. There is evidence that bones adapt to stress at muscle attachment sites associated with muscle contraction (Welten et al., 1994). However, relatively little is known about whether repeated contraction and/or strong contraction of muscles specifically leads to bone proliferation at the attachment sites. Thus it remains to be established whether relative muscle size is actually reflected by the relative sizes of muscle attachment areas.

It should be emphasized that as we develop techniques for measuring tendon moment arms in living and fossil hominoid hands we should begin to compare species in measurements for functional muscle groups, rather than focus solely upon skeletal dimensions relating to single muscles. The reason is that species are likely to share some moment arm advantages in individual muscles because of either convergences in behavior or advantages of similar morphology to different behaviors. However, they are less likely to share full sets of skeletal configurations associated with muscle mechanics because of differences among them in their overall locomotor and manipulative behaviors. The correlations of potential torque values among three sets of thumb intrinsic muscles in our chimpanzee sample suggests one possible functional group that should be investigated comparatively as additional PCSA and moment arm data are

acquired. Our preliminary data on two gorilla, one orangutan, and three hylobatid specimens in fact indicate differences among ape species in the relative sizes of both muscle PCSAs and their moment arms, in some cases approaching the difference between humans and chimpanzees for the samples reported here. We predict that some baboon species with thumb/finger proportions approaching those of humans may also share with humans moment arm advantages for muscles involved in pinching small objects between the thumb and index finger. Predictions of manipulative capabilities from skeletal predictors of moment arm lengths should also become increasingly reliable as our kinematic data are analyzed for additional regions of the hand.

CONCLUSIONS

The major distinction between chimpanzees and humans in the potential torque of thumb muscles shared by the two species appears to be mainly in the large number of longer moment arm lengths for humans, and does not arise from PCSA differences to as great an extent. Most of these moment arm differences are highly significant ($p < .01$) for our comparative sample. Force potential (PCSA) is larger in humans for only two of the shared muscles (APO and OP). Nevertheless, potential torque (the product of PCSA and moment arm) is significantly larger in humans for four muscles in trapeziometacarpal abduction/adduction (APO, FPBs, OP, and EPL), five muscles in trapeziometacarpal flexion/extension (APT, APO, OP, APB, APLm) and for one muscle (APO) in metacarpophalangeal flexion/extension.

An exception to human dominance in potential torque capabilities is the significantly larger chimpanzee PCSA and trapeziometacarpal adduction moment arm and torque for the transverse adductor pollicis muscle (APT). This contrasts in particular with the reverse condition for the adjacent oblique portion of the adductor pollicis muscle.

An interesting finding is the consistent difference between the chimpanzee sample and humans in secondary functions of the muscles at the trapeziometacarpal joint. The

chimpanzee adductors tend to flex the joint, the abductors to extend, the short flexor and opponens to adduct and the long extensor to abduct the thumb metacarpal. The reverse activities have been reported for humans. These differences in secondary functions may be related to differences in the underlying skeletal morphology and topography of the hand affecting the tendon moment arms, and thus may have important ramifications on grip capabilities and joint movements involving the full musculo-skeletal complex.

This evidence for the important contribution of tendon moment arm lengths to differences between species in muscle torque points the way toward a potentially productive new source of clues to manipulative capabilities in fossil hominoid hands. There should be a careful and extensive search for skeletal features and orientations that affect the tendon moment arm lengths, and quantitative comparison of these features in large samples of living species. In particular, the search should target features associated with groups of muscles with known complementary functions. The search will succeed only in conjunction with continued research into muscle activity, grips and hand movements associated with the wide range of manipulative activities found in living catarrhines.

ACKNOWLEDGMENTS

We thank G.L. Niebur of the Mayo Clinic Orthopedic Biomechanics Laboratory for the kinematic analysis programs used for our chimpanzee sample, and F.M. Schultz of the same laboratory for adapting the experimental apparatus to nonhuman hands. The drawing of the apparatus is by S. Selkirk. S.W. Carmichael, Ph.D. kindly provided dissection facilities in the Mayo Clinic Medical Sciences Anatomy Department. We thank D.R. Fisher for coordinating access to the specimens, and the Mayo Clinic Hand Fellows and medical student who helped at several stages of the experiment. The chimpanzee specimens were made available by the University of Texas M.D. Anderson Cancer Center Department of Veterinary Sciences, the Indiana University Department of Pathology, and the Yerkes Primate Research Center. Additional specimens for the pilot study were provided by the Primate

Foundation of Arizona, whose Institutional Animal Care and Use Committee (IACUC) reviewed and approved the animal data collection portion of the protocol. M. Rose and two anonymous reviewers provided very helpful comments on the manuscript. We also thank E. Sarmiento for careful review and criticism of an early draft of the manuscript.

LITERATURE CITED

- An K-N, Horii E, Ryu J. 1991. Muscle function. In: An K-N, Berger RA, Cooney III WP, editors. *Biomechanics of the wrist joint*. New York: Springer-Verlag. p 157-169.
- An K-N, Jacobsen MC, Berglund L, Chao EYS. 1988. Application of a magnetic tracking device to kinesiologic studies. *J Biomech* 21:613-620.
- An K-N, Takahashi K, Harrigan TP, Chao EYS. 1984. Determination of muscle orientations and moment arms. *J Biomech Eng* 106:280-282.
- An K-N, Ueba Y, Chao EYS, Cooney WP, Linscheid RL. 1983. Tendon excursion and moment arm of index finger muscles. *J Biomech* 16:419-425.
- Brand PW, Hollister A. 1993. *Clinical mechanics of the hand*, 2nd. St. Louis: Mosby Year Book.
- Brand PW, Beach RB, Thompson DE. 1981. Relative tension and potential excursion of muscles in the forearm and hand. *J Hand Surg* 6:209-219.
- Bruce P, Simon J, Oswald T. 1997. *Resampling Stats users guide*. Arlington, VA: Resampling Stats Inc.
- Chao EYS, An K-N, Cooney WP III, Linscheid RL. 1989. *Biomechanics of the hand*. Singapore: World Scientific.
- Christel M. 1993. Grasping techniques and hand preferences in Hominoidea. In: Preuschoft H, DJ Chivers, editors. *Primate hands*. New York: Springer-Verlag. p 91-108.
- Cooney WP III, Chao EY. 1977. Biomechanical analysis of static forces in the thumb during hand functions. *J Bone Joint Surg* 59A:27-36.
- Edgington E. 1995. *Randomization tests*. New York: Marcel Dekker.
- Jungers WL, Susman RL. 1984. Body size and skeletal allometry in African apes. In: Susman RL, editor. *The pygmy chimpanzee. Evolutionary biology and behavior*. New York: Plenum Press. p 131-178.
- Landsmeer JMF. 1961. Studies in the anatomy of articulation. I. The equilibrium of the "intercalated" bone. *Acta Morph Neerl-Scand* 3:287-303.
- Linscheid RL, An K-N, Gross M. 1991. Quantitative analysis of the intrinsic muscles of the hand. *Clin Anat* 4:265-284.
- Marzke MW. 1971. Origin of the human hand. *Am J Phys Anthropol* 34:61-84.
- Marzke MW. 1997. Precision grips, hand morphology and tools. *Am J Phys Anthropol* 102:91-110.
- Marzke MW, Shackley MS. 1986. Hominid hand use in the Pliocene and Pleistocene: Evidence from experimental archaeology and comparative morphology. *J Hum Evol* 15:439-460.
- Marzke MW, Wullstein KL. 1996. Chimpanzee and human grips: A new classification with a focus on evolutionary morphology. *Int J Primatol* 17:117-139.
- Marzke MW, Toth N, Schick K, Reece S, Steinberg B, Hunt K, Linscheid RL. 1998. EMG study of hand muscle recruitment during hard hammer percussion of Oldowan tools. *Am J Phys Anthropol* 105:315-332.

- Mooney CZ, Duval RD. 1993. Bootstrapping. Newbury Park: London. Sage Publications.
- Napier JR. 1962. Fossil hand bones from Olduvai Gorge. *Nature* 196:409–411.
- Napier JR. 1964. The locomotor functions of hominids. In: Washburn SL, editor. *Classification and human evolution*. New York: Wenner-Gren Foundation for Anthropological Research. p 178–189.
- Ou CA. 1979. The biomechanics of the carpometacarpal joint of the thumb. Ph.D. Dissertation. Louisiana State University, Baton Rouge.
- Rafferty KL. 1998. Structural design of the femoral neck in primates. *J Hum Evol* 34:361–383.
- Ricklan DE. 1987. Functional anatomy of the hand of *Australopithecus africanus*. *J Hum Evol* 16:643–664.
- Ricklan DE. 1990. The precision grip in *Australopithecus africanus*: Anatomical and behavioral correlates. In: Sperber GH, editor. *From apes to angels: Essays in anthropology in honor of Phillip V. Tobias*. New York: Wiley-Liss. p 171–183.
- Sarmiento EE. 1994. Terrestrial traits in the hands and feet of gorillas. *Am Museum Nov* 3091:1–56.
- Simon JL. 1974–1997. *Resampling Stats: The New Statistics*, Version 4.0.7. Arlington, VA. Resampling Stats Inc.
- Smutz WP, Kongsayreepong A, Hughes RE, Niebur G, Cooney WP, An K-N. 1998. Mechanical advantage of the thumb muscles. *J Biomech* 31:565–570.
- Susman RL. 1988a. Hand of *Paranthropus robustus* from Member 1, Swartkrans: Fossil evidence for tool behavior. *Science* 240:781–784.
- Susman RL. 1988b. New postcranial remains from Swartkrans and their bearing on the functional morphology and behavior of *Paranthropus robustus*. In: Grine F, editor. *Evolutionary history of the “robust” Australopithecines*. New York: Aldine de Gruyter. p 149–172.
- Susman RL. 1989. New hominid fossils from the Swartkrans Formation (1979–1986 excavations): Postcranial specimens. *Am J Phys Anthropol* 70:451–474.
- Tuttle RH. 1967. Knuckle-walking and the evolution of hominoid hands. *Am J Phys Anthropol* 26:171–206.
- Tuttle RH. 1969. Quantitative and functional studies of the hands of the Anthropoidea. *J Morph* 128:309–364.
- Tuttle RH. 1970. Postural, propulsive, and prehensile capabilities in the cheiridia of chimpanzees and other great apes. In: Bourne GH, editor. *The chimpanzee*, Vol. 2. Basel: Karger. p 167–253.
- Welten DC, Kemper HCG, Post GB, van Mechelen W, Twisk J, Lips P, Teule GJ. 1994. Weight-bearing activity during youth is a more important factor for peak bone mass than calcium intake. *J Bone Min Res* 9:1089–1096.
- Wilkinson JL. 1953. The insertions of the flexors pollicis et digitorum profundus. *J Anat* 87:75–88.
- Zajac FE. 1992. How musculotendon architecture and joint geometry affect the capacity of muscles to move and exert force on objects: A review with application to arm and forearm tendon transfer design. *J Hand Surg* 17:799–804.